DIETARY OVERLAP BETWEEN MOUNTAIN WAGTAILS *MOTACILLA CLARA*, GREY WAGTAILS *M. CINEREA* AND GREEN SANDPIPERS *TRINGA OCHROPUS* IN ETHIOPIA

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The extent of competition between animal species has been widely debated (Pianka 1976, Wiens 1977, Diamond 1978, Schoener 1982). General indications are that con-generics occupy 'realized' niches which allow resource partitioning, whilst the co-occurrence of more distantly related groups can result in interference or exploitation competition (e.g. Eadie & Keast 1980, Hurlbert *et al.* 1986). Resource availability can, however, prevent competition except during 'lean' periods (Schoener 1982).

One particularly interesting case of animal co-existence involves birds migrating from the northern winter into the range of related species at more southern latitudes (Moreau 1972, Keast & Morton 1980). In a previous paper (Tyler & Ormerod 1986) we have discussed this phenomenon in wagtails *Motacilla* spp., particularly with respect to the resident Mountain Wagtail *M. clara* and the migrant Grey Wagtail *M. cinerea* in Ethiopia. These two species occupy rivers in the highlands of eastern Africa when the former is breeding, but show no inter-specific aggression and little mutual exclusion. Moreover, other riverine birds, such as sandpipers Tringinae, also share the same habitat.

In this paper we examine the diet and foraging ecology of the Mountain and Grey Wagtail, and the Green Sandpiper *Tringa ochropus* as observed during December 1986 to January 1987. In particular, we test the hypothesis that their co-existence is facilitated by food partitioning. These dietary data are the first available for these species of wagtail in eastern Africa.

STUDY AREA AND METHODS

Observations were made of foraging behaviour and feeding rates of Grey and Mountain Wagtails on watercourses in two areas in highland Ethiopia in December 1986 and January 1987.

One river was situated on the eastern edge of Addis Ababa in Shewa province (9°02′N, 38°42′E, 2300 m), flowing through grassland and scrub, heavily used by grazing stock. Occasional fig trees *Ficus sycamorus* and mutilated *Acacia* grew by the river but trees had been cleared from most of the 3 km surveyed. Water levels were low and much of the river bed (5–10 m in width) was dry, the river being reduced to a series of deep pools with a narrow trickle of water flowing over algae-covered rocks; elsewhere the river was 3–4 m wide over a stoney bed. Casual inspections of the stones and rocks in the river indicated abundant invertebrates including mayfly nymphs (Ephemeroptera), caddis larvae (Trichoptera), dipteran larvae (Chironomidae and Simulidae), dragonflies (Odonata) and corixids. Amphibian tadpoles were also numerous. Clouds of midges hung over the river and were preyed upon by African Rock Martins *Hirundo fuligula*, Red-rumped Swallows *H. daurica* and African Sand Martins *Riparia paludicola*, which were nesting in riverside rocky cliffs and in banks. Other birds feeding in or over the river included Wattled Ibis *Bostrychia carunculata* and Sacred Ibis *Threskiornis aethiopica*, numerous Green Sandpipers, smaller numbers of Common Sandpipers *Actitis hypoleucos*, and two other

species of wagtail—*M. alba* the White Wagtail and *M. flava* the Yellow Wagtail. The river was heavily used by local people for washing clothes and watering stock.

The second area, at Wondo Genet (*c.* 2000 m) was on a steep, wooded escarpement south of Shashamanne (7°13′N, 38.33′E) in the Rift Valley. Here, two turbulant, rocky streams flowed down from a remnant of indigenous highland forest (*Podocarpus*), through small cultivated clearings. A series of hot springs fed into the river, and irrigation channels diverted water to crops. This resulted in areas of damp grassland adjacent to the rivers. A thick shrub and tree cover bordered, and often overhung, most of the 3–4 km surveyed. In addition to *M. clara* and *M. cinerea*, only one Green Sandpiper and a Half-collared Kingfisher *Alcedo semitorquata* were seen along these mountain rivers. Mayfly nymphs, freshwater limpets, freshwater shrimps *Gammarus*, large crustaceans (crabs) and whirligig beetles were numerous.

Methods

Visits were made on three mornings between 06:00 and 11:00 to the Addis Abab river, whereas the streams at Wondo Genet were visited in the evening and in the early morning on two consecutive days. The numbers of wagtails along survey stretches were noted. Any wagtail that was encountered was observed until it moved out of sight. Data were collected on feeding behaviour (picking from rocks in the river bed, aerial flycatching, etc.) and peck rates. Faecal material was also collected, mainly when it was possible to identify the species of bird from which it had originated, but some was collected from unidentified wagtails (*M. calra* or *M. cinerea*). Pellets regurgitated by Green Sandpipers were also collected along the Addis river and from a nearby concrete sewage lagoon, where the only visible invertebrates were mosquito larvae.

Faecal and regurgitated samples were preserved on-site in 70 per cent ethanol. Each was deflocculated for 4–8 h in 0·5M sodium hydroxide solution before examination at magnifications of x 40 to x 100. Aquatic invertebrates were identified to family and quantified by counting head capsules or mouthparts (i.e. two mandibles = 1 prey item), whilst adult insects were identified to order from recognizable parts of their wings, elytra or thoracic segments. Quantification was achieved by scoring key structures, such as sections of wing vein. Some items, such as worm chaetae or lepidopteran scales, were difficult to quantify and, where they occurred, it was assumed that one item had been ingested.

RESULTS

Density

Similar numbers of *clara* and *cinerea* occurred on the rivers surveyed, although *cinerea* was less frequent than *clara* on one of the two streams at Wondo Genet. The Mountain Wagtails were in obvious pairs and males were heard singing.

Table 1. Abundances of *M. clara* and *M. cinerea* along two rivers

River	km	*M. cinerea*	*M. clara*
Addis Ababa	3	3–4	4 (2 pairs)
Wondo Genet	3–4	3–4	7 (3 pairs)

As previously noted (Tyler & Ormerod 1986), *M. cinerea* frequently fed within 1 m of *clara* with little sign of conflict. Only on one occasion was any aggression noted by *cinerea* towards *clara*: this incident occurred immediately after an *alba* chased the *clara*, and at the same time disturbed the *cinerea*.

Foraging behaviour

At Addis, both species of wagtail fed predominantly by walking or running, mostly along shingle or on rocks, but sometimes on the grassy river bank. Prey items were pecked from water and rock surfaces, or from amongst vegetation. Short flights were occasionally made to catch prey but true aerial fly-catching was rarely observed (Table 2). Grey Wagtails were also twice observed turning over leaves.

Pecking rates did not differ significantly between the two species (a mean of 15 pecks/min in *clara* and 14·8 pecks/min in *cinerea*; n >30 in both species); since both are similar in weight and hence energy requirements, we infer that prey sizes were also similar.

Table 2. Feeding methods in *M. clara* and *M. cinerea*

Species	Total	Picking	Jumping	Aerial	s
M. cinerea	402	393	1	8	1630
M. clara	422	417	1	4	1715

At Wondo Genet both species fed predominantly from rocks in the river; *clara* picked insects from overhanging leafy branches as *cinerea* does in its breeding areas (pers. obs.), whereas *cinerea* sometimes fed up to 100 m away from the river corridor on wet grassland 'lawns' and tracks.

Diet

Foraging locations and apparent prey size indicated that simuliids or chironomids formed a major part of the diet. Faecal analysis confirmed that adult dipterans were the most common prey of both *clara* and *cinerea*. Mayfly nymphs and adults also figured prominently (Table 3). Scales of a lepidopteran were found in one faecal pellet of a *clara*, and a *cinerea* was observed catching an orange pierid butterfly *Pholotis* sp. The diet of *cinerea* also included crustacea.

Green Sandpiper pellets included Ephemeropterans and Trichopterans as the most abundant prey (Table 4). Pellets from the sewage lagoon contained only remains from mosquito larvae.

Although these data are few and were collected over a very limited time, the results indicate a great similarity in the foraging behaviour and diet of the resident Mountain and the migrant Grey Wagtails on highland rivers in Ethiopia. The limited aggression would also suggest that there is little or no interference competition between them (Tyler & Ormerod 1986). One possibility is that these species can coexist during the northern winter because this period in the highlands of Ethiopia is characterized by a super-abundance of food (Schoener 1982). However, other possibilities include niche segregation (e.g. Alatalo *et al.* 1987) with the highly flexible *cinerea* foraging outside the river corridor (pers. obs.). Alternatively, competition could occur in ways not directly

Table 3. Numbers of prey items (percentage in parentheses) taken by Mountain and Grey Wagtails as shown by faecal analysis during December 1986 and January 1987

Prey	*M. clara*	*M. cinerea*	Mixed
Trichoptera (Hydropsychidae)	10 (3·3)	4 (2·1)	
Ephemeroptera nymphs			
Ecdyonuridae	2 (0·6)		
Ephemeerellidae?	6 (2·0)	34 (19·2)	46 (10·7)
Baetidae	54 (17·7)	18 (10·1)	60 (13·9)
Ephemeroptera adults			
Caenidae	20 (6·6)	10 (5·6)	14 (3·3)
Plecoptera (Perlidae)	6 (2·0)	2 (1·1)	
Diptera larvae			
Simuliidae	10 (3·3)	16 (9·0)	
Chironomidae	2 ((0·6)	4 (2·2)	
Diptera adults*	160 (52·6)	60 (33·8)	241 (56·1)
Lepidoptera	2 (0·6)		
Coleoptera larvae	4 (1·3)	8 (4·1)	20 (4·6)
Coleoptera adults	28 (9·2)	20 (11·2)	48 (11·1)
Crustaceans (*Gammarus*?)			1 (0·6)
Total no. of prey items	304	177	429

*including Chironomidae and Empididae; 'mixed' refers to *Motacilla* faecal pellets of uncertain origin

Table 4. Prey items taken by Green Sandpipers as shown by analysis of regurgitated pellets

Prey item		No. in river[1]
Trichoptera: Hydropsychidae?		66 (25·21)
Ephemeroptera: Ephemerellidae		64 (24·4)
	Baetidae	88 (33·6)
Hemiptera: Corixidae		12 (4·6)
Coleoptera		6 (2·3)
Plecoptera		1 (0·4)
Odonata		1 (0·4)
Diptera:	Simuliidae	14 (5·4)
	adults	2 (0·8)
Mollusca (Planorbidae)		8 (3·0)
Total number of items		262

[1]From sewage, no recognizable items other than sclerites from Culicidae were found

obvious during this study. For example, Gustafsson (1987) showed that interspecific competition between tits and Collared Flycatchers *Ficedula albicollis* resulted in impaired reproductive success. *M. clara* breeds during the time that *M. cinerea* is present in Ethiopia and it is possible that if any competition occurs between the two this may be manifest in reduced brood size or chick growth, and a consequent depression of the population of *clara* by *cinerea*.

Clearly, more data are required on these aspects of motacillid ecology, in the absence of which we are unable to support any of these hypotheses. More radically, it may not be necessary to invoke competition in influencing the ecology of migrant and resident birds in Africa: their population dynamics could be affected by predation or other environmental factors. The same conclusions could apply to interactions between motacillids and other riverine birds such as Green Sandpipers, although at least in this case dietary segregation appears to be sufficient to offset any likelihood of competition.

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